BIOLOGICAL BULLETIN

OF THE

Marine Biological Laboratory

WOODS HOLE, MASS.

Editorial Staff

E. G. CONKLIN—*Princeton University.*

JACQUES LOEB—*The Rockefeller Institute for Medical Research.*

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Managing Editor

FRANK R. LILLIE—*The University of Chicago.*

VOLUME XXXIII.

WOODS HOLE, MASS.

JULY TO DECEMBER, 1917

PRESS OF
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LANCASTER, PA.

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Editorial Staff

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Managing Editor

Frank R. Lillie—*The University of Chicago.*

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BIOLOGICAL BULLETIN

THE MARINE BIOLOGICAL LABORATORY

NINETEENTH REPORT; FOR THE YEAR 1916

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I. TRUSTEES

AUGUST, 1916

EX OFFICIO

FRANK R. LILLIE, *Director*, The University of Chicago.
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D. BLAKELY HOAR, *Treasurer*, 161 Devonshire St., Boston, Mass.
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ERWIN F. SMITH.....United States Department of Agriculture.
E. B. WILSON.....Columbia University.

II. ACT OF INCORPORATION

No. 3170.

COMMONWEALTH OF MASSACHUSETTS

Be It Known, That whereas Alpheus Hyatt, William Sanford Stevens, William T. Sedgwick, Edward G. Gardiner, Susan Minns, Charles Sedgwick Minot, Samuel Wells, William G. Farlow, Anna D. Phillips

and B. H. Van Vleck have associated themselves with the intention of forming a Corporation under the name of the Marine Biological Laboratory, for the purpose of establishing and maintaining a laboratory o· station fo· scientific study and investigation, and a school for instruction in biology and natural history, and have complied with the provisions of the statutes of this Commonwealth in such case made and provided, as appears from the certificate of the President, Treasurer, and Trustees of said Corporation, duly approved by the Commissioner of Corporations, and recorded in this office;

Now, therefore, I, HENRY B. PIERCE, Secretary of the Commonwealth of Massachusetts, *do hereby certify* that said A. Hyatt, W. S. Stevens, W. T. Sedgwick, E. G. Gardiner, S. Minns, C. S. Minot, S. Wells, W. G. Farlow, A. D. Phillips, and B. H. Van Vleck, their associates and successors, are legally organized and established as, and are hereby made, an existing Corporation, under the name of the MARINE BIOLOGICAL LABORATORY, with the powers, rights and privileges, and subject to the limitations, duties, and restrictions, which by law appertain thereto.

Witness my official signature hereunto subscribed, and the seal of the Commonwealth of Massachusetts hereunto affixed, this twentieth day of March, in the year of our LORD ONE THOUSAND, EIGHT HUNDRED AND EIGHTY-EIGHT.

HENRY B. PIERCE,

(Seal). *Secretary of the Commonwealth.*

III. BY-LAWS OF THE CORPORATION OF THE MARINE BIOLOGICAL LABORATORY

I. The annual meeting of the members shall be held on the second Tuesday in August, at the Laboratory, in Woods Hole, Mass., at 12 o'clock noon, in each year, and at such meeting the members shall choose by ballot a Treasurer and a Clerk, who shall be, *ex officio*, members of the Board of Trustees, and Trustees as hereinafter provided. At the annual meeting to be held in 1897, not more than twenty-four Trustees shall be chosen, who shall be divided into four classes, to serve one, two, three, and four years, respectively, and thereafter not more than eight Trustees shall be chosen annually for the term of four years. These officers shall hold their respective offices until others are chosen and qualified in their stead. The Director and Assistant Director, who shall be chosen by the Trustees, shall also be Trustees, *ex officio*.

II. Special meetings of the members may be called by the Trustees, to be held in Boston or in Woods Hole at such time and place as may be designated.

III. The Clerk shall give notice of meetings of the members by publication in some daily newspaper published in Boston at least fifteen days before such meeting, and in case of a special meeting the notice shall state the purpose for which it is called.

IV. Twenty-five members shall constitute a quorum at any meeting.

V. The Trustees shall have the control and management of the affairs of the Corporation; they shall present a report of its condition at every annual meeting; they shall elect one of their number President and may choose such other officers and agents as they may think best; they may fix the compensation and define the duties of all the officers and agents; and may remove them, or any of them, except those chosen by the members, at any time; they may fill vacancies occurring in any manner in their own number or in any of the offices. They shall from time to time elect members of the Corporation upon such terms and conditions as they may think best.

VI. Meetings of the Trustees shall be called by the President, or by any two Trustees, and the Secretary shall give notice thereof by written or printed notice sent to each Trustee by mail, postpaid. Seven Trustees shall constitute a quorum for the transaction of business. The Board of Trustees shall have power to choose an Executive Committee from their own number, and to delegate to such Committee such of their own powers as they may deem expedient.

VII. The President shall annually appoint two Trustees, who shall constitute a committee on finance, to examine from time to time the books and accounts of the Treasurer, and to audit his accounts at the close of the year. No investments of the funds of the Corporation shall be made by the Treasurer except approved by the finance committee in writing.

VIII. The consent of every Trustee shall be necessary to dissolution of the Marine Biological Laboratory. In case of dissolution, the property shall be given to the Boston Society of Natural History, or some similar public institution on such terms as may then be agreed upon.

IX. These By-Laws may be altered at any meeting of the Trustees, provided that the notice of such meeting shall state that an alteration of the By-Laws will be acted upon.

X. Any member in good standing may vote at any meeting, either in person or by proxy duly executed.

IV. THE TREASURER'S REPORT

Statement of Audit

February 28, 1917.

Mr. D. Blakely Hoar,
161 Devonshire Street,
Boston.

Dear Sir: We have completed our audit of the accounts of the Marine Biological Laboratory for the year ended December 31, 1916, as kept both at your office in Boston and at Woods Hole and report thereon in the accompanying exhibits and schedules:

Exhibit *A*—Balance-Sheet as of December 31, 1916.
B—Income-and-Expense for Year ended December 31, 1916.

Schedule I—Investments (Book Values).
II—Cash Receipts and Payments on Account of Investments.
III—Summary of Inventory of Land, Buildings, and Equipment.
III*a*—Inventory of Land, Buildings, and Equipment, January 1, 1916.
IV—Balancing Account.

We certify that subject to the comments herewith the balance-sheet and income-and-expense statement shown herewith in Exhibits *A* and *B* are in accordance with the books and correct to the best of our knowledge and belief.

Very respectfully,
Harvey S. Chase & Company,
Certified Public Accountants.

Note: Schedules II–IV are omitted in the following reports.

Marine Biological Laboratory Balance-Sheet, December 31, 1916

Assets

Cash in Bank	$ 3,322.96	
Petty Cash at Woods Hole	200.00	$ 3,522.96
Accounts receivable		5,942.01
Investments (Schedule I)	$ 11,086.01	
Investment cash (Schedule II)	678.54	11,764.55

Inventories (not available)		
Plant account (Schedule III):		
Land	$ 78,406.29	
Buildings	163,848.88	
Equipment	73,303.36	
	$315,558.53	
Less reserve for depreciation	6,942.12	308,616.41
		$329,845.93
Liabilities and Surplus		
Accounts payable		$ 90.58
Suspense items		3.26
Notes payable	$ 3,000.00	
Turst funds	8,764.55	11,764.55
Mortgage on Gansett property		16,409.82
Balancing account		301,577.72
		$329,845.93

MARINE BIOLOGICAL LABORATORY INCOME AND EXPENSE FOR YEAR ENDED DECEMBER 31, 1916

	Expense	Income	Loss	Gain
Administration expense	$ 6,923.92		$ 6,923.92	
BIOLOGICAL BULLETIN	2,679.84	$ 1,534.08	1,145.76*	
Boat department expense	5,023.09		5,023.09	
Carpenter department	781.98	82.02	699.96	
Chemical department expense	1,455.45		1,455.45	
Dormitories	1,667.98	1,550.80	117.18	
Fish trap	1,348.68	1,406.92		$ 58.24
Interest on notes payable	150.00		150.00	
Instruction	4,075.70	5,075.00		999.30
Lectures, philosophical	100.00		100.00	
Lectures, evening	52.80		52.80	
Library department	3,447.37		3,447.37	
Mess	14,737.68	14,636.16	101.52	
Membership dues		980.00		980.00
Maintenance, buildings and grounds	6,180.18		6,180.18	
New Laboratory expense	2,636.11		2,636.11	
Pumping station expense	542.01		542.01	
Research income		3,650.00		3,650.00
Sundry expense and income	1,239.12	2,765.24		1,526.12
Supply department	13,838.43	21,096.65		7,258.22
Special dormitory expense, Dexter House	1,122.31		1,122.31	
Total expense	$68.002.65	$52,776.87	$29,697.66	$14,471.88
Total income	52,776.87		14,471.88	
Excess of expense	$15,225.78		$15,225.78	
Contribution by Mr. C. R. Crane	20,000.00			
Excess carried to balancing account	$ 4,774.22			

*Membership dues which are credited to the BIOLOGICAL BULLETIN reduce the actual deficit to $165.76.

Marine Biological Laboratory Investments (Book Values), December 31, 1916

Reserve Fund

$3,000 American Telephone & Telegraph Company, 4's (represented by receipts for same as collateral)	$2,921.25	
3/4 of $500 Western Telephone & Telegraph Company's 5's	372.66	
6 shares American Smelting & Refining Company Preferred (represented by receipts for same as collateral)	732.00	
8 shares General Electric Company	972.05	
14 shares United Shoe Machinery Company Preferred	393.75	
5 shares Massachusetts Gas Companies, Preferred	444.63	$ 5,836.34

Lucretia Crocker Fund

1/5 of $1,000 American Telephone & Telegraph Company, 4's	$ 194.75	
18 shares Vermont & Massachusetts Railroad Company	2,416.50	
1 share American Telephone & Telegraph Company	127.06	
1 share West End Street Railway Company	83.00	
2½ shares General Electric Company	323.85	3,145.16

Library Fund

4/5 of $1,000 American Telephone & Telegraph Company, 4's	$ 779.00	
1/4 of $500 Western Telephone & Telegraph Company, 5's	124.22	
3 shares American Telephone & Telegraph Company	381.18	
1 share American Smelting & Refining Company, Preferred	122.00	
2½ shares General Electric Company	288.10	
5 shares United Shoe Machinery Company, Preferred	140.63	
3 shares Massachusetts Gas Companies, Preferred	269.38	2,104.51
Total (Exhibit *A*)		$11,086.01

V. THE LIBRARIAN'S REPORT

August 8, 1916

As compared with last year, all numbers cataloged in the library make a total of 12,615. Of this total the following are new accessions:

Journals and serials from societies, laboratories, etc.	583
Books	84
Reprints	777
Last installment of A. M. N. H. loan	1,125

With the help of Prof. R. W. Tower, librarian of the American Museum of Natural History, who has been exceptionally generous in his coöperation, practically the entire loan has been placed on

our shelves. Professor Tower has agreed to send to the library as received the current parts of 32 exchanges listed as follows:

Amer. Phil. Soc. Proc.,
Amsterdam, Verh. K. Akad. Wetenschappen,
Arkiv f. Botanik,
Arkiv f. Zoologi,
Ann. Soc. Zoöl. et Malacol. de Belgique,
Bull. Soc. Roy. de Botan. de Belgique,
Canadian Entomologist,
Bull. Int. Acad. Cracovie,
Dublin, Scientific Proc. Roy. Soc.,
Proc. Roy. Soc. Edinburgh,
Trans. and Proc. Botan. Soc. Edinburgh,
Berichte d. Naturf. Gesell. Freiburg,
Journ. Linnean Soc. London,
Proc. Roy. Soc. London, Ser. B,
Trans. Zoöl. Soc. London,
Mem. and Proc. Manchester Literary and Phil. Soc.,
Trans. and Rep. Manchester Micr. Soc.,
Annales du Mus. d'Hist. Nat. Marseilles,
Medd. K. Vetenskapsakad. Nobelinstitut,
Journ. N. Y. Botan. Gard.,
Bull. Mus. Hist. Nat. Paris,
Atti d. Soc. Toscana Pisa,
Sitzungsber. d. K. B. ges. d. wiss. Math. Natur. Classe, Prag.,
Bull. Acad. Imp. Sci. St. Petersburg,
Memoirs Acad. Imp. Sci. St. Petersburg,
Stettiner Entomol. Zeitung,
K. Svenska Ver. Akad. Aarsbok,
K. Svenska Vet. Akad. Handlingar,
Boll. Mus. Zoöl. Comp. Anat. Torino,
Sitzungsber. Akad. wiss. Math. Naturw. Klasse, Wien,
Verhandlungen K. K. Zool. Bot. Gesell., Wien.

2,269 volumes and parts of volumes have been accessioned. 867 of these were bound when received. In order to care for the remainder, 656 volumes had to be bound this year, which about doubled our usual binding bill, adding to it $667.59. (This with

$171.90 previously expended for a former installment of this loan, makes a total cost for binding of $839.49.) In addition to the above, the American Museum has also given about 1,000 pamphlets that have not been cataloged.

A considerable addition will be made to the library through the sale of duplicate material representing a value of about $350. The details of this will be announced later.

A number of gifts have been made to the library which are greatly valued. From publishers, whose works are especially well placed for examination here, we have received the following:

Open Court Publishing Co., 2 books,
Cambridge University Press, 31 books,
Saunders, 1 book,
University of Chicago Press, 2 books.

Books have been received from authors as follows: A. P. Mathews, C. M. Child, J. M. Coulter, C. F. Chamberlain, M. F. Guyer, F. D. Woods, H. H. Donaldson, Henry Kraemer, C. J. Herrick, J. F. Abbott, H. E. Jordan, J. S. Ferguson, and Ramon y Cajal.

Miss Foot presented a long series of papers by Boveri and Whitman and Dr. F. R. Lillie has given 10 miscellaneous volumes.

777 reprints have been given by a long list of authors, among whom are especially to be mentioned 19 English writers: Wm. Bateson, L. Doncaster, E. S. Goodrich, W. Woodland, A. D. Cotton, W. M. Tattersall, W. E. Shipley, R. Gurney, T. V. Hoggson, Sir Charles Elliot, R. C. Punnett, T. Johnson, Richard Elmhist, J. F. Gemmill, F. Jeffrey Bell, W. B. Benham, A. Willey, W. A. Herdman, and Arnold T. Watson.

Occasion is taken here to thank the other numerous donors whose names may not be given for lack of space.

Among miscellaneous gifts are 16 volumes of the *Biochemische Zeitschrift* from Dr. A. R. Moore, which will be of great value in starting this new set. The Wistar Institute Monographs have been presented by Dr. Greeman, and the Rockefeller Institute has given a set of the Rockefeller Institute Studies. The Surgeon-General's Library has also presented Series 2 of the Index Catalog, which fills a long felt need.

Dr. Drew has deposited with the library his valuable collection of reprints and these have been in constant use this summer.

Under the head of journals and serials from museums, academies, laboratories, etc., the following sets have been completed this year:

Journal of Medical Research,
Zeit. f. Biochem. u. Biophysik,
Kansas University Science Bulletin.

223 volumes have been added during the year to incomplete sets.

The 31 serials listed below were not on our shelves last year:

Univ. Calif. Pub. in Physiology,
Univ. Cal. Pub. in Botany,
Bull. Soc. Roy. de botan. de Belgique,
Mem. Soc. Roy. de Liége,
Bull. Mus. d'hist. nat. Paris,
Abh. Naturwiss. Vereins zu Bremen,
Mem. and Proc. Manchester Literary and Phil. Soc.,
Proc. Roy. Soc. London, Sec. B,
Verhandlungen Zool. Botan. Gesell. Wien,
Sitzungsber. K. Akad. wiss. Wien,
Mem. Soc. Nat. Kiew,
Sitzungsber. Naturforsch. Gesell. Dorpat,
Ann. Mus. Zool. Acad. Imp. Sci. St. Petersburg,
Bull. Acad. Imp. Sci. St. Petersburg,
Mem. Acad. Imp. Sci. St. Petersburg,
Annals Scottish Nat. Hist. Soc.,
Proc. Roy. Soc. Edinburgh,
Sitzungsber. K. B. Gesell. wiss. Prag,
Verh. Natur. wiss. Vereins Heidelberg,
Math. u. Naturwiss. Berichte aus Ungarn,
Berichte d. Naturfor. Gesell. Freiburg,
Verh. K. Akad. Wetensch. Amsterdam,
Proc. Roy. Dublin Soc.,
Atti Soc. Toscana Pisa,
Boll. Mus. Zool. Comp. Anat. Torino,
K. Svenska Vet. Akad. Aarsbok,
K. Svenska Vet. Akad. Handlingar,
Medd. Vet. Akad. Noberinstitut.

We have also entered subscriptions for new journals as follows:

Zeit. f. induk. abstamm. u. vererbungslehre,

Genetics,
Journ. Med. Res.,
Physiological Abstracts,
Biochem. Zeitschrift.

One new exchange with the BIOLOGICAL BULLETIN has been arranged: *Bulletin de la Societé Zool. de France.*

Dr. H. H. Donaldson has generously sent a check to cover the cost of a new Century Dictionary, which has been greatly needed.

Attention is called here to our collection of photographs of foreign laboratories secured by exchange. It is planned to extend this collection to include other laboratories.

It was pointed out last year that four years ago a fund was started to aid us in extending the journal files. Last year the subscriptions to this fund had reached the sum of $91. This year a much larger group of investigators (60) whose names follow, continuing Dr. Tashiro's lead, contributed in amounts from 50 cents to $2.00. A total of $53.00 has been received in this way to date.

W. C. Allee,
Ezra Allen,
F. H. Adler,
G. A. Baitsell,
R. H. Bowen,
C. B. Bridges,
R. A. Budington,
G. L. Carver,
Eleanor Carothers,
C. M. Clapp,
C. M. Child,
C. L. Chapin,
E. J. Cohn,
M. Copeland,
E. V. Cowdry,
I. J. Davies,
G. A. Drew,
D. J. Edwards,
W. E. Garrey,
R. S. Lillie,
Jacques Loeb,
E. J. Lund,
Clara J. Lynch,
E. P. Lyon,
E. E. MacMorland,
C. E. McClung,
T. H. Morgan,
Stewart Mudd,
W. J. V. Osterhout,
Charles Packard,
B. M. Patten,
C. L. Parmenter,
Florence Peebles,
A. Richards,
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M. F. Guyer,	M. W. Welch,
L. V. Heilbrunn,	D. H. Wenrich,
Mary J. Hogue,	Paul S. Welch,
E. R. Hoskins,	H. L. Wieman,
J. S. Huxley,	W. H. Weston,
F. R. Lillie,	Miss A. E. Woodward.

Dr. Bumpus contributed $25 and Doctors Meigs, A. G. Mayer, and Knower added $10 each toward completing the sums previously promised by them. In this way the total amount of $108 was received this year. In addition there are still a few subscriptions expected from promises already published.

This fund represents a most important coöperative spirit in the development of the library. The library is used more now than ever before, as witnessed by the fact that 350 books were charged in one day. Never before have so many individuals of the Laboratory shown their appreciation of the library by voluntarily contributing to its support and extension. Such wide interest on the part of so many members of the Laboratory leading to numerous small gifts, whether in money or books, will be of the greatest value to the library. It is much appreciated! All the more because it is so broadly coöperative!

It is to be hoped that the Laboratory can soon supplement these gifts and place at the disposal of the library a sum to be expended in emergencies for the purchase of bargains which often become unexpectedly available. Such a fund of say $300 a year would make it possible to fill in gaps, complete sets, and add works which would be difficult to secure through more regular and slower channels. There is no more urgent need of the library than the maintenance of such an emergency fund, now so well started.

VI. THE DIRECTOR'S REPORT

To the Trustees of the Marine Biological Laboratory:

Gentlemen: I have the honor to present a report of the twenty-ninth session of the Marine Biological Laboratory for the year 1916. The total attendance was slightly smaller than in 1915, 231 as compared with 242, but larger than that of any earlier year. There were 129 investigators and 102 students, a falling off of 8 in the number of investigators and of 3 in the number of students. The decrease in investigators falls entirely under the head of investigation under instruction; indeed the number of independent investigators shows a gain of 5. The decrease should therefore be regarded as probably of a fluctuating character, as the group concerned consists largely of research students of members of the independent group of investigators. The slight decrease in student attendance was due entirely to our method of registration, for the number of applicants for courses was larger than ever before; after the courses were registered to the limit of our accommodations many students were refused registration. Later some of those registered failed to appear. It is obvious, therefore, that heads of departments should be allowed to register in excess of accommodations to a certain extent, in the expectation that a certain proportion of those registered will finally be unable to attend. The past season is the first one in which registration in advance was positively required, and this was done because the experience of 1915 had shown that unlimited registration was likely to exceed capacity, as indeed the number of applications in 1916 actually showed.

In spite of the slight decrease in numbers there was an increase in the receipts from investigators and students over all previous sessions, viz.: $8,725 in 1916 as compared with $8,325 in 1915, $7,300 in 1914, $6,160 in 1913, and $5,175 in 1912. The gain was entirely from the research side due to the fact that coöperating institutions subscribed $800 more in 1916 than in 1915 ($5,000 as against $4,200). The number of subscribing institutions was 40 in 1916 and 37 in 1915. The Supply Department has again shown a large increase of sales, which amounted to $21,096.65,

as against $16,932.00 in 1915, $14,003.35 in 1914, $14,554.40 in 1913, $13,966.35 in 1912, $10,303.61 in 1911. The business has actually doubled in the last six years.

For several years the Director has called attention to need of increased accommodation for workers at the Laboratory in two directions: first the need of extra dormitory space for students, and second the need of cottages for the families of investigators, or of land on which such cottages could be placed. Both these needs now bid fair to be satisfied for some years to come. Mr. Crane has turned over to the Laboratory the Dexter House for use as a dormitory, with a sufficient sum of money to repair and equip it. We feel that with the other dormitory accommodations previously provided the students' needs will be adequately cared for. At the same time this extra accommodation enables us to dedicate the third floor of the Supply Department building, hitherto reserved for dormitory purposes, to the rapidly growing needs of this Department.

Provision has also been made for building sites for investigators by the purchase of 21 acres of woodland in the Gansett woods, immediately joining the Crow Hill region of Woods Hole, in which many of the Laboratory members now have homes, and extending from Quissett Ave. nearly to Buzzards Bay. This piece of land enjoys perpetual rights in a bathing reservation in a sandy cove of Buzzards Bay immediately adjoining. For convenience of location with reference to the Laboratory and to the sea no more desirable location could have been found; and there is no more beautiful tract in the entire town of Falmouth. Mr. Crane has furnished the money necessary to complete the purchase on favorable terms made by the owners, and he has also provided funds for its development, including the building of roads, which it is hoped may be accepted by the town. This work is now in progress, so that it is expected that parts of the land will be available for building purposes in the spring. A considerable number of requests for lots already have been received and some preliminary assignments made.

In view of the difficulty that has existed for so long in securing building sites for our membership and the probability that such difficulties are likely to increase in the future, the director

recommends that none of this land be permanently alienated from the Laboratory by outright sale; and in order that it may be reserved for the purposes for which it was acquired he also recommends that none of it be otherwise disposed of except to members of the Laboratory unless by vote of the Board of Trustees in each case. Deeds of sale should, therefore, include a claim ensuring ultimate reversion to the Laboratory on equitable terms, and provisions should also be made for long term leaseholds. The form and value of the leasehold have occasioned much thought, and certain proposals are herewith presented for consideration by the Board. The valuations have been determined with no idea of speculative gain, but solely from the point of view of covering cost and expense of development with a small margin of safety for probable slowness of development. There is room obviously for difference of opinion with reference to values set on individual lots which have been determined as nearly as possible on the basis of general desirability. It will be found on comparison that the values thus determined contrast very favorably with the prices of building lots anywhere else in Woods Hole.

There is appended as part of this report a list of the staff, of investigators and students in attendance, a tabular view of attendance covering the last five years, a list of subscribing institutions, the Evening Lectures, and the Membership of the Corporation.

1. THE STAFF

1916

FRANK R. LILLIE, DIRECTOR,
Professor of Embryology, and Chairman of the Department of Zoölogy, The University of Chicago.

GILMAN A. DREW, ASSISTANT DIRECTOR, Marine Biological Laboratory.

ZOÖLOGY

I. INVESTIGATION

GARY N. CALKINS.....Professor of Protozoölogy, Columbia University.

E. G. CONKLIN.....Professor of Zoölogy, Princeton University.
GILMAN A. DREW.....Assistant Director, Marine Biological Laboratory.
GEORGE LEFEVRE.....Professor of Zoölogy, The University of Missouri.
FRANK R. LILLIE.....Professor of Embryology, The University of Chicago.
C. E. MCCLUNG.....Professor of Zoölogy, University of Pennsylvania.
T. H. MORGAN.....Professor of Experimental Zoölogy, Columbia University.
E. B. WILSON.....Professor of Zoölogy, Columbia University.

II. INSTRUCTION

CASWELL GRAVE.....Associate Professor of Zoölogy, Johns Hopkins University.
W. C. ALLEE.....Professor of Biology, Lake Forest College.
GEORGE A. BAITSELL.....Instructor in Biology, Yale University.
ROBERT HALL BOWEN.....Graduate Student, Columbia University.
W. J. KOSTIR.....Instructor in Zoölogy and Entomology, Ohio State University.
T. W. PAINTER.....Adjunct Professor of Zoölogy, University of Texas.
FRANCIS M. ROOT.....Bruce Fellow, Johns Hopkins University.

EMBRYOLOGY

I. INVESTIGATION (See Zoölogy)

II. INSTRUCTION

WILLIAM E. KELLICOTT.....Professor of Biology, Goucher College.
ROBERT A. BUDINGTON.....Professor of Zoölogy, Oberlin College.
CHARLES PACKARD.....Instructor in Zoölogy, Columbia University.
CHARLES G. ROGERS.....Professor of Zoölogy, Oberlin College.
REYNOLD A. SPAETH.....Instructor in Biology, Yale University.

PHYSIOLOGY

I. INVESTIGATION

ALBERT P. MATHEWS.....Professor of Physiological Chemistry, The University of Chicago.
RALPH S. LILLIE.....Professor of Biology, Clark University.

HAROLD C. BRADLEY.....Assistant Professor of Physiological Chemistry, University of Wisconsin.
SHIRO TASHIRO.....Instructor in Physiological Chemistry, The University of Chicago.

II. INSTRUCTION

RALPH S. LILLIE.....Professor of Biology, Clark University.
WALTER E. GARREY.....Professor of Physiology, Tulane University.
FRANK P. KNOWLTON.....Professor of Physiology, Syracuse University.
A. R. MOORE.....Professor of Physiology, Rutgers College.

PHILOSOPHICAL ASPECTS OF BIOLOGY AND ALLIED SCIENCES

LECTURES

EDWARD G. SPAULDING....Professor of Philosophy, Princeton University.

BOTANY

GEORGE T. MOORE.....Director, Missouri Botanical Garden and Professor of Botany, Washington University.
IVEY F. LEWIS.....Professor of Biology, University of Virginia.
CARL S. HOAR.....Instructor in charge of Botany, Williams College.

LIBRARY

H. E. MCKNOWER.....Professor of Anatomy, University of Cincinnati, Librarian.
MARY E. SCOTT.....Assistant Librarian.

Chemical Supplies[1]

OLIVER S. STRONG.....Instructor in Anatomy, College of Physicians and Surgeons, New York City, Chemist.

Supply Department

G. M. GRAY.....Curator.
JOHN J. VEEDER....Captain.
E. M. LEWIS.....Engineer.
A. W. LEATHERS...Collector.
A. M. HILTON.....Collector.
F. G. GUSTAFSON...Collector in Botany.
EDNA E. WELLS....Clerk.

[1] Compound microscopes, with two oculars and two objectives, rack and pinion and fine adjustment, may be rented for the seasons at $7.00 each, provided notice is received by the assistant director not later than June 15.

F. M. MacNaught.....Business Manager.
Herbert A. Hilton....Superintendent of Buildings and Grounds.

2. INVESTIGATORS AND STUDENTS

1916

ZOÖLOGY

Independent Investigators

Addison, William H. F., Assistant Professor of Normal Histology and Embryology, University of Pennsylvania.
Allee, Warder C., Professor of Biology, Lake Forest College.
Allen, Ezra, Honorary Fellow, University of Pennsylvania.
Baitsell, George A., Instructor in Biology, Yale University.
Binford, Raymond, Professor of Zoölogy, Earlham College.
Bridges, Calvin B., Columbia University.
Budington, Robert A., Professor of Zoölogy, Oberlin College.
Calkins, Gary N., Professor of Protozoölogy, Columbia University.
Carothers, E. Eleanor, University of Pennsylvania.
Carver, Gail L., Professor of Biology, Mercer University.
Chidester, Floyd E., Associate Professor of Zoölogy, Rutgers College.
Child, Charles M., Associate Professor of Zoölogy, University of Chicago.
Clapp, Cornelia M., Professor Emeritus, Mount Holyoke College.
Conklin, E. G., Professor of Biology, Princeton University.
Copeland, Manton, Professor of Biology, Bowdoin College.
Cowdry, Edmund V., Associate in Anatomy, Johns Hopkins Medical School.
Cowdry, N. H., Johns Hopkins Medical School.
Crampton, H. E., Professor of Zoölogy, Barnard College, Columbia University.
Donaldson, Henry H., Professor of Neurology, Wistar Institute.
Drew, Gilman A., Assistant Director, Marine Biological Laboratory, Woods Hole.
Gee, Wilson, Professor of Biology, Emory University.
Goldfarb, A. J., Assistant Professor of Biology, College of the City of New York.
Goldschmidt, Richard, Kaiser Wilhelm Institut für Biologie.
Goodrich, Hubert B., Instructor in Biology, Union College.
Grave, Caswell, Associate Professor of Zoölogy, Johns Hopkins University.
Gregory, Emily R., University of Pennsylvania.
Gross, Alfred O., Assistant Professor of Zoölogy, Bowdoin College.
Guyer, Michael F., Professor of Zoölogy, University of Wisconsin.
Heilbrunn, Lewis V., Associate in Embryology, University of Chicago.
Hogue, Mary J., Instructor in Zoölogy, Wellesley College.
Hoskins, Elmer R., Instructor in Anatomy, New York University.
Jacobs, Merkel H., Assistant Professor of Zoölogy, University of Pennsylvania.
Kellicott, William E., Professor of Biology, Goucher College.
Kernall, Morris J., University of Illinois.
Knower, Henry McE., Professor of Anatomy, University of Cincinnati.
Lefevre, George, Professor of Zoölogy, University of Missouri.
Lillie, Frank R., Professor of Embryology, University of Chicago.
Lund, Elmer J., Assistant Professor of Zoölogy, University of Minnesota.

McCLUNG, CLARENCE E., Director of Zoölogy Laboratories, University of Pennsylvania.
MALONE, EDWARD F., Associate Professor of Anatomy, University of Cincinnati.
MOODIE, ROY L., Associate in Anatomy, University of Illinois.
MOORE, CARL R., Assistant in Embryology, University of Chicago.
MORGAN, THOMAS H., Professor of Experimental Zoölogy, Columbia University.
MORRIS, MARGARET, Yale University.
MULLER, HERMANN J., Instructor, Rice Institute.
NEWMAN, HORATIO H., Associate Professor of Zoölogy, University of Chicago.
PACKARD, CHARLES, Instructor in Zoölogy, Columbia University.
PAPPENHEIMER, ALVIN M., Assistant Professor of Pathology, Columbia University.
PATTEN, WILLIAM, Professor of Biology, Dartmouth College.
PEEBLES, FLORENCE, Professor of Biology, H. Sophie Newcomb Memorial College.
REAGEN, F. P., Princeton University.
RICHARDS, A., Adjunct Professor of Zoölogy, University of Texas.
ROGERS, CHARLES G., Professor of Comparative Physiology, Oberlin College.
SHULL, A. FRANKLIN, Associate Professor of Zoölogy, University of Michigan.
SHUMWAY, WALDO, Instructor in Biology, Amherst College.
SPAETH, REYNOLD A., Instructor in Biology, Yale University.
SPAULDING, EDWARD G., Professor of Philosophy, Princeton University.
STOCKARD, CHARLES R., Professor of Anatomy, Cornell Medical College.
STRONG, OLIVER S., Instructor in Anatomy, Columbia University.
STRONG, ARCHIBALD M., Instructor in Medicine, Columbia University.
STURTEVANT, ALFRED H., Columbia University.
TAYLOR, HERBERT D., Assistant in Pathology and Bacteriology, Rockefeller Institute.
TENNENT, DAVID H., Professor of Biology, Bryn Mawr College.
WENRICH, DAVID H., Instructor in Zoölogy, University of Pennsylvania.
WEINSTEIN, ALEXANDER, Fellow, Columbia University.
WELCH, PAUL S., Associate Professor of Entomology, Kansas State Agricultural College.
WHITING, PHINEAS W., Research Fellow, University of Pennsylvania.
WIEMAN, HARRY L., Head of Dept. of Zoölogy, University of Cincinnati.
WILSON, E. B., Professor of Zoölogy, Columbia University.
WOODWARD, ALVALYN E., Instructor, Vassar College.

Beginning Investigators

BLAKE, IRVING H., Dept. of Zoölogy and Physiology, Oregon Agricultural College.
BRUMFIEL, DANIEL M., Instructor in Animal Biology, University of Iowa.
CHAPIN, CATHARINE L., University of Chicago.
COHN, EDWIN J., University of Chicago.
DAVIES, I. J., Micrologist, Rice Institute.
GLOBUS, JOSEPH H., Assistant in Anatomy, Cornell Medical School.
GOLDMAN, AGNES, Cornell Medical School.
HEILBRUNN, STELLA, Teacher, Bay Ridge High School, Brooklyn.
HERMAN, WILLIAM, Harvard Medical School.
HOY, WILLIAM E., JR., Instructor, University of Rochester.
HUXLEY, JULIAN S., Assistant Professor of Biology, Rice Institute.
LYNCH, CLARA J., 945 W. Cleveland Ave., Canton, Ohio.

MacArthur, John W., Associate in Zoölogy, University of Chicago.
MacMorland, Edward E., Fellow in Biology, Princeton University.
Cooper, Arthur R., Fellow in Zoölogy, University of Illinois.
Minoura, Tadachika, University of Chicago.
Montgomery, Mrs. Priscilla B., University of Pennsylvania.
Parmenter, Charles L., Assistant, University of Minnesota.
Pinney, Mary E., Demonstrator in Biology, Bryn Mawr College.
Root, Francis M., Fellow, Johns Hopkins University.
Safir, Shelley R., Teacher in Stuyvesant High School, New York City.
Smith, Christianna, Assistant, Zoölogy Department, Mt. Holyoke College.
Speidel, Carl C., Graduate Student, Princeton University.
Ware, Clara C., Assistant at Barnard College, Columbia University.
White, Edith G., Research Assistant, Princeton University.

PHYSIOLOGY

Independent Investigators

Chambers, Robert, Jr., Instructor in Anatomy, Cornell Medical College.
Day, Edward C., Lecturer in Physiology, Bryn Mawr College.
Duesberg, Jules, Research Associate, Carnegie Institution.
Edwards, Dayton J., Instructor in Physiology, College of City of New York.
Ellis, Frederick W., Monson, Mass.
Garrey, Walter E., Professor of Physiology, Tulane University.
Harvey, E. Newton, Assistant Professor of Physiology, Princeton Univ.
Harvey, Mrs. E. Newton, Princeton, N. J.
Knowlton, Frank P., Professor of Physiology, Syracuse University.
Kudo, R., Rockefeller Institute for Medical Research.
Lillie, Ralph S., Professor of Biology, Clark University.
Loeb, Jacques, Head of Department of Experimental Biology, Rockefeller Institute for Medical Research.
Lyon, Elias P., Professor of Physiology, University of Minnesota.
Mathews, Albert P., Professor of Physiological Chemistry, University of Chicago.
Moore, Arthur R., Professor of Physiology, Rutgers College.
Noguchi, Hideyo, Research Member, Rockefeller Institute for Medical Research.
Northrop, John H., Assistant, Rockefeller Institute for Medical Research.
Patten, Bradley M., Senior Instructor, Western Reserve Medical School.
Price, Weston A., Chairman, Research Commission of the National Dental Association, Cleveland, Ohio.
Richards, Annabella E., Demonstrator of Chemistry, Woman's Medical College of Pennsylvania.
Rudisch, Julius, Consulting Physician, Mount Sinai Hospital, New York.
Van der Stricht, O., Western Reserve Medical School.
Wasteneys, Hardolph, Associate in Experimental Biology, Rockefeller Institute for Medical Research.

Beginning Investigators

Adler, Francis H., University of Pennsylvania.
Chamberlain, Mary M., Fellow, University of Pennsylvania.
Noble, Arlyle, Assistant in Bacteriological Research, Parke Davis & Co.

BOTANY

Independent Investigators

LEWIS, IVEY F., Professor of Biology, University of Virginia.
LYMAN, GEORGE R., Pathological Inspector, Dept. of Agriculture, Washington, D. C.
MOORE, GEORGE T., Director, Missouri Botanical Garden, St. Louis, Mo.
MOORE, EMMELINE, Instructor, Vassar College.
OSTERHOUT, W. J. V., Professor of Botany, Harvard University.
SNOW, LAETITIA M., Associate Professor of Botany, Wellesley College.
WESTON, WILLIAM H., JR., Instructor in Biology, Adelbert College.

Beginning Investigator

HAAS, ALBERT R., Graduate Student, Harvard University.

STUDENTS

1916

BOTANY

BROWNING, HAROLD W., University of Wisconsin, Madison, Wis.
CLUM, HAROLD H., Student, Oberlin College, Oberlin, Ohio.
DONOVAN, STEPHEN M., Student, St. Bonaventure, St. Bonaventure, N. Y.
DE ANGULO, MRS. CARY F., Carmel, California.
FURBER, JANE M., 769 Washington St., Brookline, Mass.
JONES, WINIFRED, Teacher, Cincinnati Public Schools, Cincinnati, Ohio.
MCNAIR, FRANCES D., Smith College, Northampton, Mass.
MCWHORTER, FRANK P., Vanderbilt University, Nashville, Tenn.
MARTIN, GEORGE W., Instructor, Mass. Agricultural College, Amherst, Mass.
PAGE, FREDERICK S., Instructor, Dartmouth College, Hanover, N. H.
REEVES, WALTER S., Missouri Botanical Garden, St. Louis, Mo.
SMITH, EDNA L., Carmel, California.

EMBRYOLOGY

BAKER, ETHEL C., 123 Chiswick Road, Boston, Mass.
BEYER, HENRY G., U. S. Navy, Retired.
BODINE, JOSEPH H., Assistant in Zoölogy, University of Pennsylvania.
BOWEN, ROBERT H., 330 Summit Ave., Mt. Vernon, N. Y.
CHARLTON, HARRY H., North Billerica, Mass.
DRUIEN, MILDRED M., Vassar College, Poughkeepsie, N. Y.
HAGUE, FLORENCE, Assistant, Kansas State Agricultural College.
HOAGLAND, RUTH A., Assistant in Zoölogy, Vassar College.
HOPKINS, HOYT S., Johns Hopkins University, Baltimore, Md.
JOB, THESLE T., Fellow, State University of Iowa.
LOPEZ-SUAREZ, JUAN, Madrid.
MCROBERTS, EARL S., Butler College, Indianapolis, Ind.
MAHR, ERNEST F., Syracuse University, Syracuse, N. Y.
MASON, MICHAEL L., Northwestern University.
MOORE, DOROTHEA M., Radcliffe College, Cambridge, Mass.

MYERS, DOROTHY K., Barnard College, New York City.
PARKER, SYLVIA L., Laboratory Assistant, Mt. Holyoke College.
RAE, ANNE M., Teacher, Girls High School, Brooklyn, N. Y.
RIPPLE, C. VINCENT, Instructor, South Philadelphia High School.
ROWLAND, EDITH L., Barnard College, New York City.
SCHNEIDER, PETER A., Instructor, University of Vermont.
SHAW, MYRON E., Student, Carleton College.
SMITH, ELIZABETH A., Instructor in Zoölogy, University of Wisconsin.
SPROWLES, EDITH A., Teacher, Frankford High School, Frankford, Pa.
VAUPEL, JEAN, University of Cincinnati.
WARDWELL, EDWARD H., Graduate Student, Brown University.

PHYSIOLOGY

CHASE, SAMUEL W., Student, Harvard University.
CHILDS, HENRY E., Teacher, Rochester, N. Y.
GREISHEIMER, ESTHER, Clark University.
HUNT, HARRISON R., Student, Harvard University.
IRWIN, MARION, 53 Garden St., Cambridge, Mass.
MILLIKIN, FRANCES, Smith College, Northampton, Mass.
MUDD, STUART, Princeton, N. J.
MÜHL, ANITA M., Butler College, Indianapolis, Ind.
POND, SAMUEL E., Fellow, Clark University.
RUNYON, PAUL M., Student, Princeton University.
SAMPSON, MYRA M., Instructor, Smith College.
TWINING, RALPH H., Clark University.
YOUNG, PAUL T., Graduate Student, Princeton University.
YOUNG, ELDRID G., 4876 Sherbrooke St., Montreal.

ZOÖLOGY

BACH, ELLEN B., 721 S. Ingalls St., Ann Arbor, Mich.
BARGEN, JACOB A., Student, Carleton College.
BICKERSTAFF, FLORENCE W., Student, Oberlin College.
BIDDLE, M. GEORGINA, 2017 De Lancey Place, Philadelphia, Pa.
BLATCHFORD, BARBARA, Student, Vassar College.
BRENTON, THADDEUS R., Laboratory Assistant in Zoölogy, Moores Hill College.
BRUMBACK, FLORENCE M., Teacher, Waukegan Township High School.
BRUNSWICK, MARK, Quissett, Mass.
BRYANT, GLADYS, Student, Radcliffe College.
CHOATE, MABEL, Barnard College, Columbia University.
CAULDWELL, OLIVIA, Student, Vassar College.
COLVILL, HELEN, Teacher, Circleville, Ohio.
DAVIS, GORDON E., Oberlin College.
DAWSON, JAMES A., Assistant in Biology, Yale University.
DETWILER, SAMUEL R., Graduate Student, Yale University.
DE LA CRUZ, Dionysia G., Student, Sophie Newcomb College.
ELLINGER, MARGARET, 14 W. 25th St., Baltimore, Md.
FELTY, AUGUSTUS R., 734 Prospect Ave., Hartford, Conn.
HERRICK, RUTH, University of Chicago.
HINRICHS, MARIE A., 1832 Blue Island Ave., Chicago, Ill.

HOULDING, ERNEST W., 182 E. College St., Oberlin, Ohio.
LAMB, LAURA, 527 S. 41st St., Philadelphia, Pa.
LEVIEN, EUNICE M., Lake Forest College.
LEIGH, HOWARD, Earlham College.
MACK, RUTH J., Radcliffe College, Cambridge, Mass.
NEUN, ELSIE G., University of Rochester.
NUTE, BERTHA E., Mount Holyoke College.
ROACH, ETHEL S., University of Rochester.
RORER, MARY D., Student, Mount Holyoke College.
ROWE, GEORGIA M., 2321 N. Calvert St., Baltimore, Md.
RUHL, REBECCA L., 205 E. Main St., Clarksburg, W. Va.
SEAGO, MARY M., Student, Sophie Newcomb College.
SKILLERN, INEZ, Sweet Briar College, Sweet Briar, Va.
STEWART, ELEANOR G., 425 St. Clair St., Pittsburgh, Pa.
STEWART, FRED W., Schuyler Fellow, Cornell University.
SWANN, MRS. ARTHUR W., 124 East 61st St., New York City.
TAYLOR, MARTHA, Student, Radcliffe College.
TILGHMAN, SARAH A., Goucher College.
TURK, IRENE, Hunter College, New York City.
VERNOOY, LESTER C., Amherst College.
WAKEFIELD, LUCILE, Student, Carnegie Institute of Technology.
WALKER, LOUISE, Laboratory Assistant, Brearley School, New York City.
WALTERS, MARY J., Goucher College, Baltimore, Md.
WALTON, EVERETT P., Topsham, Maine.
WASSERMAN, JEANETTE H., Hunter College, New York City.
WHITE, GERTRUDE M., Assistant, University of Wisconsin.
WEINSTEIN, FLORENCE, Student, Barnard College.
WELCH, M. W., 1806 Morse Ave., Chicago, Ill.
WENRICH, MYRA S., Philadelphia, Pa.
YAGLE, ELIZABETH M., Student, Carnegie Institute of Technology.

3. TABULAR VIEW OF ATTENDANCE

	1912	1913	1914	1915	1916
INVESTIGATORS—Total	93	122	129	137	129
Independent:					
Zoölogy	44	58	62	69	70
Physiology	14	17	22	20	23
Botany	10	11	10	6	7
Under Instruction:					
Zoölogy	21	21	31	36	25
Physiology	2	7	1	4	3
Botany	2	7	3	2	1
STUDENTS—Total	67	69	89	105	102
Zoölogy	24	33	43	47	50

Embryology	15	22	21	37	26
Physiology	11	8	10	15	14
Botany	17	7	15	6	12
TOTAL ATTENDANCE	160	191	218	242	231
INSTITUTIONS REPRESENTED—Total	57	80	77	79	73
By investigators	43	50	51	59	51
By students	36	41	47	42	45
SCHOOLS AND ACADEMIES REPRESENTED:					
By investigators	2	3	1	3	—
By students	1	6	5	9	3

4. SUBSCRIBING INSTITUTIONS—1916

AMHERST COLLEGE
BARNARD COLLEGE
BOWDOIN COLLEGE
BRYN MAWR COLLEGE
CARLETON COLLEGE
CARNEGIE INSTITUTE OF TECHNOLOGY
CLARK UNIVERSITY
COLUMBIA UNIVERSITY
DARTMOUTH COLLEGE
ELSE SERINGHAUS SCHOLARSHIP, HUNTER COLLEGE, NEW YORK CITY
GOUCHER COLLEGE
HARVARD UNIVERSITY
JOHNS HOPKINS UNIVERSITY
KANSAS STATE AGRICULTURAL COLLEGE
KAISER WILHELM INSTITUT FÜR BIOLOGIE
LAKE FOREST COLLEGE
MOUNT HOLYOKE COLLEGE
NORTHWESTERN UNIVERSITY
OBERLIN COLLEGE
PRINCETON UNIVERSITY, DEPT. OF BIOLOGY
PRINCETON UNIVERSITY, DEPT. OF PSYCHOLOGY
RADCLIFFE COLLEGE
ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH
RICE INSTITUTE
RUTGERS COLLEGE
SMITH COLLEGE

H. SOPHIE NEWCOMB MEMORIAL COLLEGE
UNIVERSITY OF CHICAGO
UNIVERSITY OF CINCINNATI
UNIVERSITY OF ILLINOIS
UNIVERSITY OF KANSAS
UNIVERSITY OF MICHIGAN
UNIVERSITY OF PENNSYLVANIA
UNIVERSITY OF ROCHESTER
UNIVERSITY OF TEXAS
UNIVERSITY OF WISCONSIN
VASSAR COLLEGE
WELLESLEY COLLEGE
WISTAR INSTITUTE
YALE UNIVERSITY

5. EVENING LECTURES, 1916

Friday, June 30,
PROF. W. J. V. OSTERHOUT....."Permeability and Antagonism."
Friday, July 7,
PROF. JACQUES LOEB....."On Adaptation to Environment."
Tuesday, July 11,
DR. ROBERT M. YERKES....."The Study of Monkeys and Apes."
Friday, July 14,
DR. JAMES B. MURPHY....."Studies in Lymphoid Activity."
Tuesday, July 18,
PROF. ALEXANDER PETRUNKEVITCH. "Segmentation in Arthropods."
Friday, July 21,
PROF. J. LAWRENCE HENDERSON...."Organization as a Physical Chemical Problem."
Tuesday, July 25,
PROF. W. B. CANNON....."Some Recent Studies of Glands of Internal Secretion."
Friday, July 28,
PROF. RICHARD GOLDSCHMIDT....."Experimental Intersexuality and the Sex-problem."
Tuesday, Aug. 1,
DR. RAYMOND PEARL....."Parental Alcoholism and the Progeny in Poultry."

Tuesday, Aug. 8,

DR. ALFRED G. MAYER.....“Biological Problems of the Pacific.”

MEMBERS OF THE CORPORATION

LIFE MEMBERS

ALLIS, MR. E. P., JR., Palais Carnoles, Menton, France.
ANDREWS, MRS. GWENDOLEN FOULKE, Baltimore, Md.
BILLINGS, MR. R. C., 66 Franklin St., Boston, Mass.
CAREY, MR. ARTHUR ASTOR, Fayerweather St., Boston, Mass.
CLARKE, PROF. S. F., Williamstown, Mass.
CONKLIN, PROF. EDWIN G., Princeton University, Princeton, N. J.
CRANE, MR. C. R., Woods Hole, Mass.
DAVIS, MAJOR HENRY M., Syracuse, N. Y.
EVANS, MRS. GLENDOWER, 12 Otis Place, Boston, Mass.
FARLOW, PROF. W. G., Harvard University, Cambridge, Mass.
FAY, MISS S. B., 88 Mt. Vernon St., Boston, Mass.
FOLSOM, MISS AMY, 88 Marlboro St., Boston, Mass.
FOOT, MISS KATHERINE, 955 Park Ave., New York City, N. Y.
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STUDIES ON THE BIOLOGY OF PARACOPIDOSOMOPSIS II. SPERMATOGENESIS OF MALES REARED FROM UNFERTILIZED EGGS.[1]

J. T. PATTERSON AND LELIA T. PORTER.

In the first paper of this series it was pointed out that the unfertilized egg of *Paracopidosomopsis floridanus* produces a polyembryonic brood of males. It is the purpose of this paper to show that the germ cells of such males are characterized by the haploid number of chromosomes. As in many other Hymenoptera, the presence of the half number is due to the fact that in the parthenogenetic development of the matured egg there is no compensatory process for restoring the full number. As a consequence of the reduced number of chromosomes in these males, the maturation divisions are modified in such a way that two, instead of four, spermatozoa are produced from each first spermatocyte. In the somatic cells of these males the haploid number, subject to certain variations, also prevails; but this is a subject that will be considered later.

Material and Methods.

All of the material used in the study of spermatogenesis has been taken from animals reared under experimental conditions. It consists of two large broods of larvæ and a series of one hundred pupæ taken from a mummified carcass of the host. The two larval broods were preserved forty-eight and twenty-four hours, respectively, prior to the time at which pupation would have occurred. The series of pupa stages were preserved at close intervals, beginning twenty-four hours after the formation of the carcass.

The three broods yielding this material resulted from an experiment designed to determine whether the unfertilized egg

[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 131.

developed into a brood of males. A summary of the experiment is as follows:

Host eggs laid the night of November 7.
Each egg parasitized by one oviposition of an unfertilized female, 2:30 P.M., Nov. 8.
Caterpillars hatched Nov. 13.
First brood of parasites preserved Dec. 4.
Second brood of parasites preserved Dec. 5.
Carcass of third caterpillar formed Dec. 6.
Series of pupa stages from carcass preserved Dec. 7–19.
Brood of 1842 male parasites emerged Dec. 25.

We have used a great variety of fixing fluids on polyembryonic material, but for the cytology of male germ cells no reagent has been found that equals Bouin's picro-formol-acetic mixture to which crystals of urea have been added. Preparations of the gonads fixed in this fluid and treated with Heidenhain's iron hæmatoxylin, counterstained with Orange G, give very fine results. However, this method of fixation has the disadvantage of not being adapted to the staining technique usually employed to bring out certain cytoplasmic structures, such as the mitochondria. Nevertheless, we have used it almost exclusively because of our especial interest in the chromosomes.

Even with the use of the best methods of technique, Hymenoptera material is never as favorable for the study of chromosomes as that of many other insects, notably the Hemiptera and Orthoptera. In certain respects, the germ cells of *Paracopidosomopsis* are more favorable for cytological study than those of many other species of the order, but even in this species the chromosomes are, at certain stages, greatly elongated, with a consequent tendency to become entangled with one another. This often makes difficult the determination of the exact number. The difficulty is somewhat increased by the smallness of the cell, which at the end of the growth period does not exceed a diameter of seven or eight microns. The best counts of chromosome numbers are obtained in somatic cells, because in these cells the metaphase plate is flat and the chromosomes are more scattered than in the spermatocytes. In any event, one does not experience difficulty in distinguishing a metaphase plate

with the haploid number of chromosomes from one having the diploid number.

The Spermatogonia.

We have not attempted to follow closely the course of development of the male gonads in the larva. At the earliest stage at which the larva can be recognized as a male, each testis consists of a solid spherical mass of cells. Histologically, there are two kinds of cellular elements, germ cells and epithelial cells. During the course of further development the gonad elongates, and at the same time cyst formation occurs. This process is completed by the end of the larval period.

At no time during the development of the gonad does one find any great number of spermatogonial divisions. Four or five mitotic figures are the most that will be found at any one time in a given testis.

The period of multiplication ends sometime between forty-eight and twenty-four hours prior to pupation. Of the two larval broods mentioned above, the one preserved forty-eight hours before the time of pupation has a few larvæ showing spermatogonial divisions, while the one fixed twenty-four hours later has no divisions.

Fig. 1 shows a metaphase plate of one of the dividing spermatogonia. The plate has eight elongated chromosomes, one of which shows the beginning of a longitudinal split. We have concluded from a study of all of our material of both males and females that eight represents the haploid number of chromosomes.

The Growth Period.

The growth period begins shortly after the cessation of the spermatogonial divisions, and extends through the fourth day after pupation. At the beginning of this period all of the germ cells in a given cyst are in the same stage of development. In section each cell appears wedge-shaped, with its slightly curved base lying against the outer membrane and its apex directed toward the center of the cyst. The apexes of all the cells in the cyst are usually connected by a common mass, which is apparently the remains of the interzonal fibers of the last spermatogonial division.

The growth stage is characterized by the presence of a conspicuous nucleolus, which occupies an excentric position in the nucleus (Figs. 2–4). At first the nucleolus is somewhat diffuse, but later its outline becomes sharp and distinct (Fig. 2). It frequently has several less deeply stained areas lying at its center (Fig. 3). We have good reasons for believing that the nucleolus is chromatin in character.

One of the most striking changes to occur in the cell during growth, is the appearance of certain cytoplasmic inclusions, which stain intensely black with iron hæmatoxylin. These are first seen about seventy-two hours after pupation, when they appear as dark, elongated areas in the cytoplasm. Later, as the cell enlarges, the areas become more definite and appear as seen in Fig. 3. These structures soon disappear (Figs. 4, 5), although some of them may persist until after the first maturation division is well advanced (Figs. 6, 8). We have not attempted to determine the origin and nature of these cytoplasmic inclusions; but, judging from the work of Meves on the bee, they are probably mitochondrial in character.

The presence of these inclusions greatly interferes with the study of the changes which now take place in the cell. Especially is this true with reference to those changes involving the behavior of the centrosomes. We shall therefore confine our account to the changes in shape of the cell which occur during the growth period. As already stated, all of the cells of a cyst are at first united at their pointed ends by the interzonal connections. In some cells these connections are soon lost, and each cell then becomes polyhedral in outline (Figs. 2, 3), and finally spherical. In other cells the interzonal connections apparently persist throughout the entire growth period, and after these are finally severed, the pointed end of each primary spermatocyte contains the remains of the original interzonal connection in the form of an "interzonal body" (Mark and Copeland).

At the end of the growth period many cells are met with which possess a delicate process. It is difficult to demonstrate the presence of a centrosome at the end of this process (Fig. 4). With reference to the position of the cell in the cyst, the process may lie on any side of the cell. It is not clear whether such a

process is formed in every cell. If it is of constant occurrence, the period of its existence must be very brief; for at the beginning of the first spermatocyte division, which soon follows, it is entirely absent.

A similar process has been described for the young spermatocytes of several different Hymenoptera, but the most careful and detailed work on it is that of Meves ('07) on the honey bee. According to Meves, the process in the bee is formed through the influence of one of the primary centrosomes ("Hauptcentriolen"), which arise by division from the original centrosome of the cell. The process with its centrosome is soon withdrawn into the cell. One of the several secondary centrosomes ("Nebencentriolen") which had previously arisen by division from the primary centrosomes, then participates in the formation of the mitotic figure responsible for the production of the so-called polar body.

While it is not possible in our material to demonstrate all of these fine points, yet it is highly probable that the cytoplasmic process in the germ cells of *Paracopidosomopsis* has a similar history to that described by Meves for the germ cells of the bee.

First Maturation Division.

Preparation for the first maturation division is made manifest by changes in the nucleus. It is also made evident by changes in the shape of the cell, especially in the spermatocytes which have early lost their interzonal connections. In cells in which these connections persist up until the end of the growth period, the so-called polar body, or rudimentary second spermatocyte, is budded off from the side of the cell that had recently had the connection. In the other spermatocytes a blunt protrusion arises at one side (Fig. 5), which soon develops into a pointed process (Fig. 6). At the pointed end thus formed there is present a tiny centrosome, from which radiate a number of delicate fibers toward the nucleus. At the opposite, or blunt end of the cell, a similar centrosome with its fibers is also present.

The most important change in the nucleus concerns the nucleolus, which during the first half of the growth period remains a deeply staining, spherical mass (Figs. 2, 3). A number

of spherical granules arise at its periphery, giving it the appearance of a lobulated structure (Fig. 4). Eventually the nucleolus breaks up into a number of these large granules, which lie in a finely granular matrix (Fig. 5). Apparently these larger granules coalesce to form the chromosomes (Fig. 7). From a careful study of this particular stage, one can not escape the conclusion that the chromosomes arise from the nucleolus.

A somewhat similar method of origin of chromosomes has been described by Meves and Duesberg ('08) in the male germ cells of *Vespa crabro*. They say: "Das Herannalien der ersten Reifungsteilung macht sich dadurch bemerkbar, das im Kern in der Umgebung des grösseren Nucleolus immer mehr Chromatinkörner auftreten. Der Nukleolus selbst wird dabei immer kleiner. Man gewinnt den Eindruck, dass seine Substanz in diejenige der Chromatinkörner übergeht." There is one important difference between the two forms. In *Paracopidosomopsis* the nucleolus gradually but completely disappears as the chromosomes are formed, while in *Vespa* a small body still remains after the chromosomes are organized.

During the organization of the chromosomes the nucleus elongates in the direction of the long axis of the cell. An imperfect intranuclear spindle then arises, and upon this the chromosomes tend to take up an equatorial position (Figs. 6, 8). They are usually so closely massed together that it is impossible to make an exact determination of their number. Fig. 6 shows a very interesting case, in which a single curved chromosome has moved to the upper end of the nucleus, where it lies in contact with the inner surface of the nuclear membrane. On account of the massed condition of the chromosomes, it is not possible to tell whether this particular chromosome is the product of a recent division, and has a sister chromosome lying within the mass. However, this is an isolated case, and it is clear that the chromosomes do not normally divide in the first spermatocyte division. Instead, only the cytoplasm undergoes division, and this in a very adequal manner (Figs. 7, 8).

The constriction of the cytoplasm begins about one-third the distance from the pointed end of the cell (Fig. 7) and finally results in cutting off a small, knob-like mass entirely free of

chromatin (Fig. 9). This abortive division is homologous to the first spermatocyte division which normally occurs in other forms, and the two unequal cells thus produced are to be regarded as equivalent to second spermatocytes.

The small non-nucleated cell, or mass of cytoplasm, soon degenerates, although in some cases it may persist until the second maturation division is well advanced. All stages in the disintegration of the mass are to be seen in a single cyst. The fragmenting masses lie in the interstices of the dividing second spermatocytes.

The most interesting point to be noted in connection with this abortive maturation division is the fact that nothing comparable to a synapsis of chromosomes occurs. The absence of this phenomenon, which is universal in the spermatogenesis of males arising from fertilized eggs, is undoubtedly due to the fact that the unmatured, male germ cell of *Paracopidosomopsis* possesses but the haploid number of chromosomes. The function of the first maturation division is to bring about a reduction from the diploid to the haploid number of chromosomes; but the males of this species, by virtue of their origin from matured, but unfertilized eggs, already possess the half number, and consequently, the first maturation results in a feeble or abortive attempt at a division.

Second Maturation Division.

Throughout the entire period occupied by the first maturation, the nuclear membrane remains intact (Figs. 5–9). At the end of this period the incomplete intranuclear spindle disappears, as do also the fibers which radiate from the centrosome included in the small cytoplasmic mass (Fig. 9). On the contrary, the aster, which lies at the lower side of the nucleus in the true second spermatocyte, persists. It is highly probable that this aster, by a division of its centrosome, gives rise to the second maturation spindle, as is the case in the European hornet.

In the brief interim between the first and second maturations, the nucleus enters a rest stage. The chromatin recedes to that side of the nucleus lying farthest from the cytoplasmic bud, and becomes so massed that it is impossible longer to distinguish

clearly individual chromosomes (Fig. 9). In the stages immediately following this one, every phase in the reorganization of the chromosomes is clearly demonstrable. In having a definite resting stage between the abortive and the true division, *Paracopidosomopsis* resembles *Neuroterus* (Doncaster, '09), but differs from such forms as the bee and the wasp.

After the cytoplasmic bud is cut off, the second spermatocyte becomes spherical in outline, and a conspicuous maturation spindle is formed (Fig. 12). The reorganized chromosomes are drawn into the equatorial position on this spindle. Clear polar views are difficult to find, owing to the fact that the chromosomes are elongated and frequently twisted (Fig. 12). In the clearest cases observed, the number of chromosomes is seen to be eight (Figs. 10, 11).

The axis of the second maturation spindle bears no definite relation to that of the first maturation spindle. This was determined by studying those second spermatocytes to which the cytoplasmic bud remains for some time slightly attached. It was found that the axis of the second spindle has no definite relation to the point of attachment.

In the second division the chromosomes split lengthwise, and the daughter chromosomes pass to the opposite poles of the spindle (Fig. 14). It is frequently easy to count the eight daughter chromosomes passing to the one or the other of the poles, but cells in which both daughter groups can be counted are not often met with (Fig. 15). We conclude from these observations that all of the chromosomes divide in the second maturation. While in the anaphases the chromosomes are often well scattered, yet we have found no evidence of a distinctly "advancing" or "lagging" member, such as might indicate that a particular chromosome had failed to divide. From this it follows that the two spermatids resulting from the second division will be alike. That is to say, the spermatozoa in *Paracopidosomopsis* will not be dimorphic.

In passing to the poles of the spindle the chromosomes keep their long axes parallel to the long axis of the spindle (Figs. 15, 16), and upon reaching the pole fuse to form a solid, deeply staining mass of chromatin out of which the spermatid nucleus arises (Figs. 17, 18).

After the division of the cytoplasm, the two spermatids remain connected for some time by means of the interzonal fibers (Fig. 18). After they separate, each differentiates into a typical spermatozoön (Figs. 19, 20). We shall not discuss further the subject of the metamorphosis of the spermatids, except to emphasize the point that both spermatids must form functional germ cells, as we have found no evidence of degenerating spermatids or spermatozoa.

Comparison with other Hymenoptera.

Studies on the spermatogenesis of Hymenoptera have shown that there is a striking modification of the maturation process in those species in which sex-determination is supposed to be in accordance with the Dzierzon theory. Instead of four spermatozoa arising from each first spermatocyte, only one or two matured germ cells develop. In one group of these Hymenoptera both spermatocyte divisions are abortive; the first division cutting off a small cytoplasmic bud free of chromatin, and the second division a small bud which receives half the chromatin. There is thus produced but a single spermatid, and consequently only one spermatozoön. In the second group the first division is likewise abortive, producing a cytoplasmic bud, but the second division is equal, producing two similar spermatids, which metamorphose into spermatozoa.

To the first of these groups belongs the honey bee, as has been shown by the work of Meves ('03, '07), Mark and Copeland ('06), and Doncaster ('06, '07). To this class there also probably belongs the solitary bee (*Osmia cornuta*) worked on by Armbruster ('13).

The second group includes a number of different species, of which the following may be mentioned: *Xylocopa violacea* (Granata, '10, '13), *Neuroterus lenticularis* (Doncaster, '09), *Vespa crabro* (Meves and Duesberg, '08), *Vespa maculata* (Mark and Copeland, '07), *Vespa germanica* (Meves, '03), *Camponotus herculaneus* (Meves and Duesberg, '08, and Lams, '08), *Dryophanta erinacei* (Wieman, '15). *Paracopidosomopsis floridanus* also clearly belongs to this class.

While the various investigators report differences as to details

in the two types of spermatogenesis outlined above, yet there is great uniformity in their interpretations of the general character of the processes involved. Our own work on *Paracopidosomopsis* indicates that the spermatogenesis of this species is very similar, not only as regards the general character of the process, but also as regards many details, to the maturations of the European hornet, *Vespa crabro*, as shown by the work of Meves and Duesberg.

AUSTIN, TEXAS,
February 6, 1917.

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DESCRIPTION OF FIGURES.

All of the figures are camera drawings made at table level, with the Zeiss 2 mm. lens and No. 12 compensating ocular. The figures thus outlined were enlarged three times by the aid of an enlarging camera, and then reproduced with one third off. They are therefore magnified about 3857.

PLATE I.

FIG. 1. Metaphase plate of last spermatogonial division.

FIG. 2. Stage at the beginning of growt[1] period.

FIG. 3. Stage at the mid-growth period, showing the conspicuous cytoplasmic inclusions.

FIG. 4. Spermatocyte with delicate cytoplasmic process.

FIG. 5. Elongation of the cell in preparation for the first spermatocyte division.

FIG. 6. Stage showing the imperfect intranuclear spindle.

FIG. 7. Stage showing the beginning of the constriction which results in cutting off the cytoplasmic bud.

FIG. 8. A later stage showing the same process.

FIG. 9. Stage showing the end of the first maturation division. The cytoplasmic bud has just been cut off.

FIG. 10. Metaphase plate of the second spermatocyte.

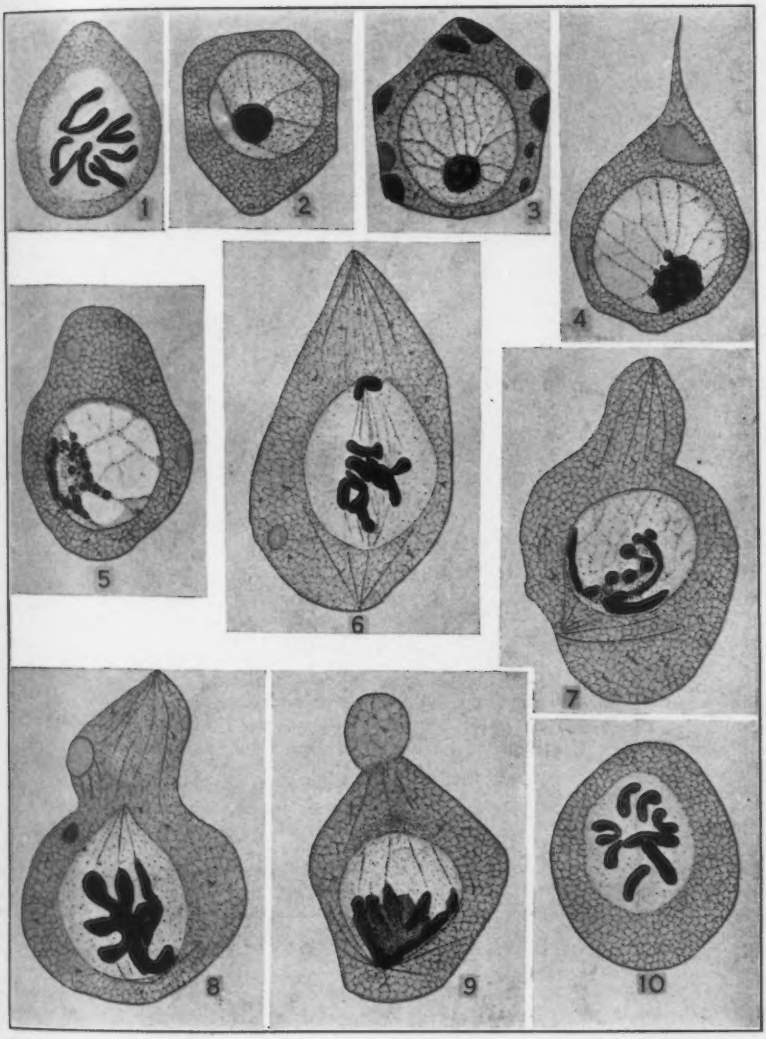

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PLATE II.

FIG. 11. Metaphase plate of the second spermatocyte.

FIG. 12. Side view of the second maturation spindle, showing four twisted chromosomes.

FIG. 13. A section through one side of the spindle, showing two chromosomes that have just divided. Parts of two other chromosomes are also present.

FIG. 14. A similar section, showing the complete division of four chromosomes.

FIG. 15. Anaphase stage, showing eight daughter chromosomes passing to each pole.

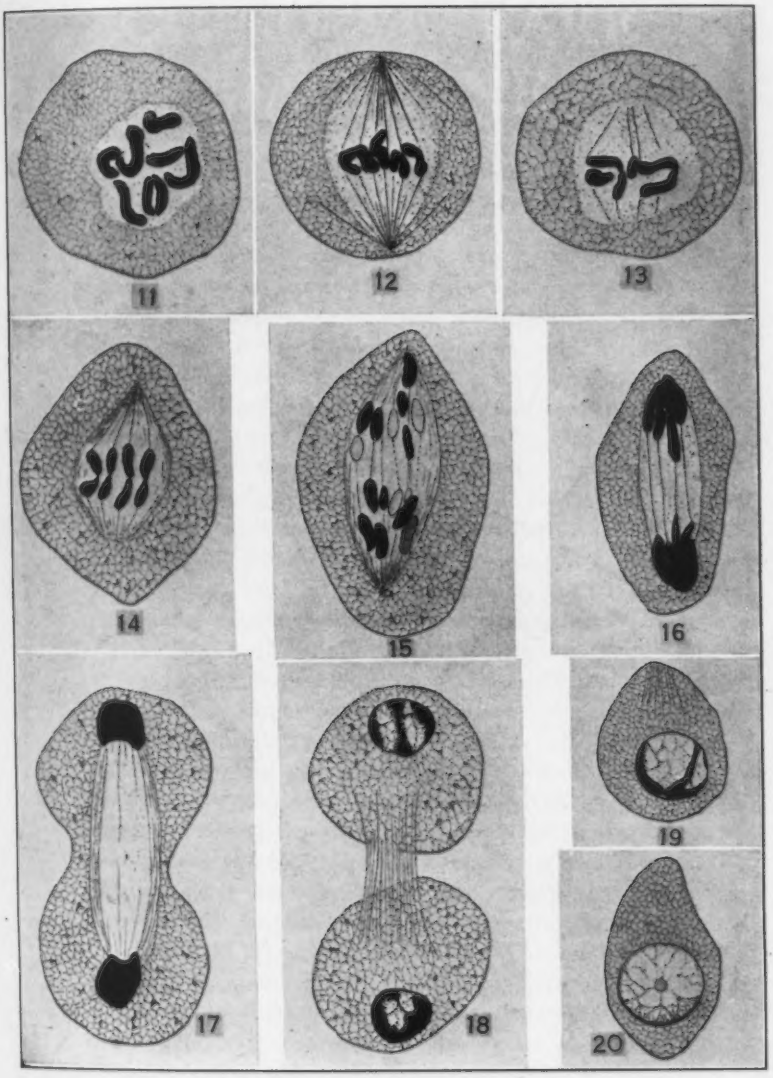
FIG. 16. Late anaphase stage.

FIG. 17. Telophase stage.

FIG. 18. The two spermatids, still connected by means of the interzonal fibres.

FIG. 19. A completely separated spermatid.

FIG. 20. A later stage of the spermatid.



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RHYTHMS AND ENDOMIXIS IN VARIOUS RACES OF PARAMÆCIUM AURELIA.

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In view of the fact that the study of rhythms and endomixis in *Paramœcium* was made chiefly on my long pedigreed race of *Paramœcium aurelia*, it has been suggested by a couple of authors that the reorganization process may be something peculiar to this race, perhaps resulting from long subjection to conditions which preclude the possibility of conjugation. This assumption, however, was rendered exceedingly improbable from the data presented by Woodruff and Erdmann[1] in their original complete paper which showed that "the same reorganization process was resumed in all the lines within a relatively short time after conjugation" was allowed to occur in a subculture of the main race, and also that the phenomenon was observed early in the culture of a race which was secured by Erdmann from Berlin, Germany. Further, Erdmann and Woodruff[2] in a paper on endomixis in *Paramœcium caudatum* stated incidentally that endomixis had been found in two new races of *Paramœcium aurelia* immediately upon their isolation.

The above data more than justify the early conclusion of Woodruff and Erdmann that "this reorganization process is a normal phenomenon and *probably occurs in all races of the species Paramœcium aurelia*," [3] but in connection with other work on *Paramœcium* it has been necessary to employ various races for study and the purpose of the present paper is to record briefly the additional data bearing on the points under discussion. This may be most readily accomplished by considering seratim the graphs of the life histories which show the rhythms and the occurrence of endomixis in the respective cultures. Since

[1] *Journal of Experimental Zoology*, Vol. 17, No. 4, 1914.

[2] *Journal of Experimental Zoology*, Vol. 20, No. 2, 1916.

[3] *Ibid.*, 1914, p. 474.

the methods of conducting the cultures, plotting the graphs, etc., has been fully described in earlier papers from this laboratory, the reader is referred to them for details of technique. It is only necessary to emphasize here that the occurrence of endo-

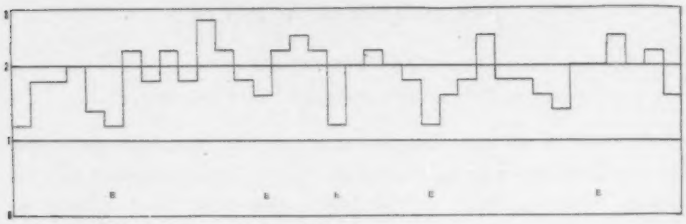

FIG. 1.

mixis has been determined, of course, in each case by the cytological study of animals preserved almost daily from each culture during the periods under discussion.

Race I. (*Woodruff's Main Culture.*)—Isolated May 1, 1907, at Williamstown, Mass., and carried in pedigreed culture to

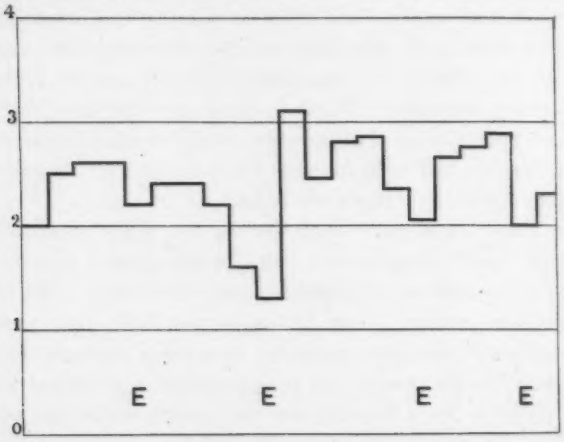

FIG. 2.

date (July, 1917). During this period of more than ten years it has attained over 6,000 generations without conjugation. The discovery of endomixis was made on this race and full details

have been presented in earlier papers. Fig. 1[1] gives a typical graph of a subculture showing the relation of rhythms and endomixis.

Race II. (*Berlin Race.*)—Isolated by Erdmann in Berlin. For details see Woodruff and Erdmann, 1914.

Race III. (*Oberlin Race.*)—The initial animals of this pedigreed culture was supplied by Professor R. A. Budington, of Oberlin, Ohio. The culture was started October 8, 1914, and was discontinued after nearly two years during which time over 1,000 generations were obtained. Fig. 2 is a graph of the average division rate of the four lines of this culture again averaged for each of the first 21 five-day periods of its life when it was being intensively studied with reference to the occurrence of rhythms and endomixis. The graph shows four rhythms and at the low point between each endomixis occurred. It is to be

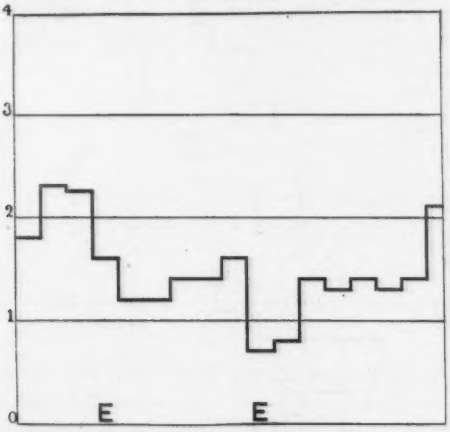

FIG. 3.

noted that the reorganization process appeared during the fifth five-day period after the isolation of the culture, thus showing once more that this phenomenon is not dependent upon long subjection to culture conditions for its genesis. The length of the rhythmic periods for this race is also essentially the same as in Race I (cf. Fig. 1).

Race IV. (*Bryn Mawr Race.*)—The animal which started

[1] *Ibid.*, 1914, Fig. 17.

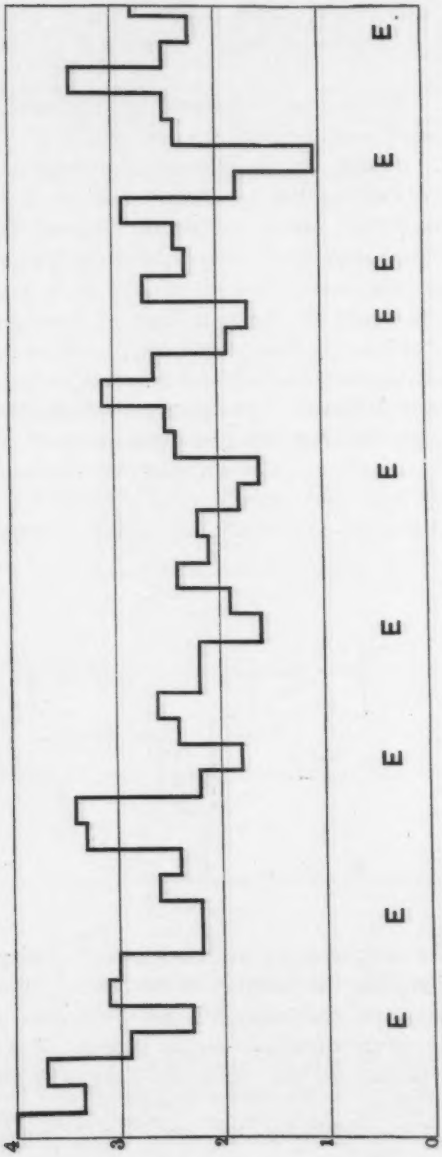

FIG. 4.

this pedigreed culture was isolated on January 7, 1915, from material supplied by Dr. Florence Peebles from Bryn Mawr, Pa. The culture was discontinued at the 650th generation on February 8, 1916. Fig. 3 shows the relationship of rhythms and endomixis during the first eighty-five days of the culture when the animals were being examined for the reorganization process. The results fully substantiate those obtained from previous races. The last inter-rhythm period shown in the diagram is apparently longer than usual—though it is possible that endomixis was overlooked about the 15th five-day period.

Race V. (*Oxford Race.*)—Culture started, from material secured at Oxford, Ohio, on July 16, 1915, and discontinued on August 7, 1916, at the 1,000th generation. The division rate of the culture is shown in Fig. 4 for the first 44 five-day periods of

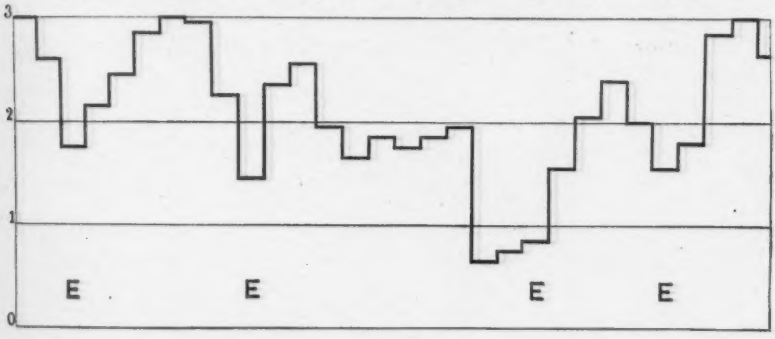

FIG. 5.

its life. During this time nine rhythms occurred at each of which endomixis was observed. It is hoped that readers who may possess doubts concerning rhythms and endomixis will carefully consider this graph.

Race VI. (*Woods Hole Race.*)—This race was obtained by Dr. G. A. Baitsell at Woods Hole, Mass., and its pedigreed culture was begun on August 11, 1915, and discontinued on January 14, 1916, at the 305th generation. Fig. 5 gives the graph of the division rate of this culture throughout its existence.[1]

[1] The division rate is plotted consistently one quarter of a division per day too fast for every five-day period, owing to a draughtsman's error. An *E* should be inserted in the first period.

Endomixis occurred as soon as the culture was started and recurred at the usual intervals. The animal was not studied cytologically during the 14th five-day period so that endomixis is not indicated by an *E* in this period on the chart, but from the character of the curve there can be little doubt that an examination of stained specimens would have revealed it.

In a word, then, the data from every culture of *Paramœcium aurelia* (isolated from as diverse localities as Ohio and Germany) which we have studied prove beyond doubt, I believe, that endomixis is a normal periodic phenomenon which occurs in all races of *Paramœcium aurelia*.